

RESEARCH ARTICLE

Visual resolution and contrast sensitivity in two benthic sharks

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ABSTRACT

Sharks have long been described as having ‘poor’ vision. They are cone monochromats and anatomical estimates suggest they have low spatial resolution. However, there are no direct behavioural measurements of spatial resolution or contrast sensitivity. This study estimates contrast sensitivity and spatial resolution of two species of benthic sharks, the Port Jackson shark, *Heterodontus portusjacksoni*, and the brown-banded bamboo shark, *Chiloscyllium punctatum*, by recording eye movements in response to optokinetic stimuli. Both species tracked moving low spatial frequency gratings with weak but consistent eye movements. Eye movements ceased at 0.38 cycles per degree, even for high contrasts, suggesting low spatial resolution. However, at lower spatial frequencies, eye movements were elicited by low contrast gratings, 1.3% and 2.9% contrast in *H. portusjacksoni* and *C. punctatum*, respectively. Contrast sensitivity was higher than in other vertebrates with a similar spatial resolving power, which may reflect an adaptation to the relatively low contrast encountered in aquatic environments. Optokinetic gain was consistently low and neither species stabilised the gratings on their retina. To check whether restraining the animals affected their optokinetic responses, we also analysed eye movements in free-swimming *C. punctatum*. We found no eye movements that could compensate for body rotations, suggesting that vision may pass through phases of stabilisation and blur during swimming. As *C. punctatum* is a sedentary benthic species, gaze stabilisation during swimming may not be essential. Our results suggest that vision in sharks is not ‘poor’ as previously suggested, but optimised for contrast detection rather than spatial resolution.

KEY WORDS: Optokinetic eye movements, Contrast sensitivity, Acuity, Spatial resolving power

INTRODUCTION

Sharks are often described as having ‘poor’ vision. This conclusion is based on their lack of colour vision (Hart et al., 2011; Schluessel et al., 2014) and low spatial resolving power (Hueter, 1990; Lisney and Collin, 2008; Litherland and Collin, 2008). Although they perceive their world through a number of other sensory modalities such as electroreception, olfaction, audition, the mechanosensory lateral line and possibly even magnetoreception (Hueter et al., 2004; Meyer et al., 2005; Gardiner et al., 2012), vision is still important for communication (Ritter and Godknecht, 2000; Martin, 2007), navigation (Parker, 1910; Fuss et al., 2014), as well as the detection and identification of prey and predators (Hobson, 1963;

Gilbert, 1970; Strong, 1996; Hammerschlag et al., 2012; Seamone et al., 2014).

The information content of vision is, to a large extent, determined by the spatial resolving power and contrast sensitivity of the eye (Eckert and Zeil, 2001; Land and Nilsson, 2012). Both contrast sensitivity and spatial resolving power influence an animal’s ability to discriminate objects against a background and affect the distance at which detection can occur (Land, 1999; Eckert and Zeil, 2001). Anatomical estimates of spatial resolving power have been obtained for a number of shark species and range from two to 11 cycles per degree (cpd) (Hueter, 1990; Lisney and Collin, 2008; Litherland and Collin, 2008). However, no estimates of contrast sensitivity or behavioural estimates of spatial resolution currently exist, suggesting that categorising sharks as having ‘poor’ vision may be presumptuous. In aquatic environments, absorption and light scattering strongly affect the visual contrast of an object as the distance from the observer increases (Lythgoe, 1980, 1988; McFarland, 1990; Land and Nilsson, 2012). Thus, underwater contrast, rather than spatial resolving power, is often the limiting factor in the early detection and identification of objects. Sharks may trade off spatial resolving power and enhance contrast sensitivity.

The contrast sensitivity function was assessed by measuring eye movements in response to computer-generated optokinetic stimuli in two benthic shark species, Port Jackson sharks, *Heterodontus portusjacksoni* (F. A. A. Meyer 1793), and brown-banded bamboo sharks, *Chiloscyllium punctatum* J. P. Müller & Henle 1838. The contrast sensitivity function is an important descriptor of the visual system as it describes contrast sensitivity as a function of spatial frequency (Land, 1999; Eckert and Zeil, 2001; Land and Nilsson, 2012). It therefore measures both spatial resolving power and contrast sensitivity.

Optokinetic experiments used to measure the contrast sensitivity function in a range of vertebrates typically have been based on a striped pattern (grating) on the inside of a rotating drum, which induces reflex eye movements aimed at stabilising the image on the retina (cat, Donaghy, 1980; primates, Miller et al., 1980; opossum, Silveira et al., 1982; chicken, Jarvis et al., 2009; and teleost fish, Fritsches and Marshall, 2002; Rinner et al., 2005). Optokinetic eye movements consist of a slow phase, in which the eyes rotate smoothly in the direction of the stimulus in order to remove the rotational component of optic flow, and a fast phase, in which a saccadic eye movement resets the eye to a more central position, often alternating repeatedly in a rhythmic pattern (Fernald, 1985; Mandecki and Domenici, 2015).

The optokinetic apparatus also provides an opportunity to investigate gaze stabilisation in sharks. Most animals move through their environment and must cope with image motion on the retina, or optic flow, which can lead to optic blur. To reduce optic blur, animals use head, eye and/or body movements to stabilise the image on the retina. A failure to stabilise gaze against background movement reduces both perceived contrast as well as spatial resolving power (Land, 1999, 2015). Eye movements can

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also be used to fixate a moving object on the most sensitive region of the retina (Collewijn, 1977; Frost, 1978; Land, 1999, 2015).

Eye movements in sharks are thought to be controlled through efference copy, a neural mechanism in which a copy of the signal that controls the movement of the tail and body during swimming is sent to the eye muscles, thereby causing eye movements that counteract body rotation (Harris, 1965; Combes et al., 2008; Land, 2015). Sharks have a unique organisation of oculomotor neurones (Graf and Brunken, 1984), suggesting that the optokinetic responses in sharks may differ from other vertebrates. Considering the phylogenetic importance of sharks in that they evolved over 400 million years ago (Miller et al., 2003) and are the oldest living descendants of the first jawed vertebrates, they may represent a phylogenetically conserved design for optokinetic eye movements (Davis et al., 2012). However, to date, no optokinetic responses have been observed in sharks (Masseck and Hoffmann, 2009; Land, 2015). The study species *H. portusjacksoni* and *C. punctatum* are the most primitive of the modern sharks (galeomorphs) (Shirai, 1992, 1996; Winchell et al., 2004). Understanding contrast sensitivity, spatial resolving power and gaze stabilisation in these species may therefore provide insights into the origins of visual perception in modern sharks and other contemporary vertebrates.

In this study, eye movements of restrained sharks were measured in response to stimuli simulating different forms of self motion: horizontal motion (translation), vertical motion and rotation around the longitudinal body axis (roll). Eye movements were also measured in free-swimming *C. punctatum* to assess the effects of restraining the animals and to estimate the impact of motion blur, by calculating the distance at which objects are stabilised on the retina during a swimming cycle.

MATERIALS AND METHODS

Ethics statement and experimental animals

Three captive-bred brown-banded bamboo sharks, *C. punctatum* [fork length (FL) 35–40 cm, eye diameter 7.5–9.5 mm], and three wild-caught Port Jackson sharks, *H. portusjacksoni* (FL 20–30 cm, eye diameter 9.5–11 mm), were used for the optokinetic

experiments. *Heterodontus portusjacksoni* were held in a large 2800 litre aquarium and *C. punctatum* were held in a 1000 litre aquarium before and after any experimental procedures. Eye movements in free-swimming individuals were only recorded from *C. punctatum*, as they were held in a glass aquarium that was suitable for the video recordings. The experiments complied with the Western Australia Animal Welfare Act (2002) and were covered by an ethics protocol (RA/3/100/1220), approved by the animal ethics committee of The University of Western Australia.

Optokinetic apparatus

During optokinetic experiments, sharks were gently restrained in a small square tank (30×25 cm) by placing small wooden pegs along the side of the body. The head and tail were secured with flexible plastic straps. A 1 cm clear Perspex plate in front of the shark maintained the animal's head 5 cm from the front edge of the tank. The tank was positioned in the centre of four radiance-calibrated LCD computer monitors (Dell E2310Hc, Dell Inc.) with the midpoint between the animals' eyes positioned 25 cm away from all monitors (Fig. 1A,B). The monitors had a light intensity of $3.2 \times 10^{-5} \text{ W sr}^{-1} \text{ cm}^{-2}$, measured using a calibrated light meter (International Light Technologies, ILT1700). The monitors covered approximately 65 deg of the sharks' vertical visual field and 360 deg of their horizontal field. The visual fields of the species used in this study have not been measured, but the monitors would have covered approximately 68% of the total visual field of a lemon shark (*Negaprion brevirostris*), which have comparable eye position to the species used in this study (McComb et al., 2009).

All visual stimuli were constructed in MATLAB (The MathWorks, Natick, MA, USA) utilising the Psychtoolbox 3 extension (Brainard, 1997; Pelli, 1997). Eye movements were recorded using a Sony Handycam (HDR CX700 or HDR CX550) set to night mode and positioned below the monitor. Infrared LED (850 nm) lights aided the detection of the pupil, without affecting the light intensity perceived by the sharks. Videos were converted to avi format using FFmpeg (git-1654ca7; <https://www.ffmpeg.org/>) and imported into a custom MATLAB program (J.M.H.; modified

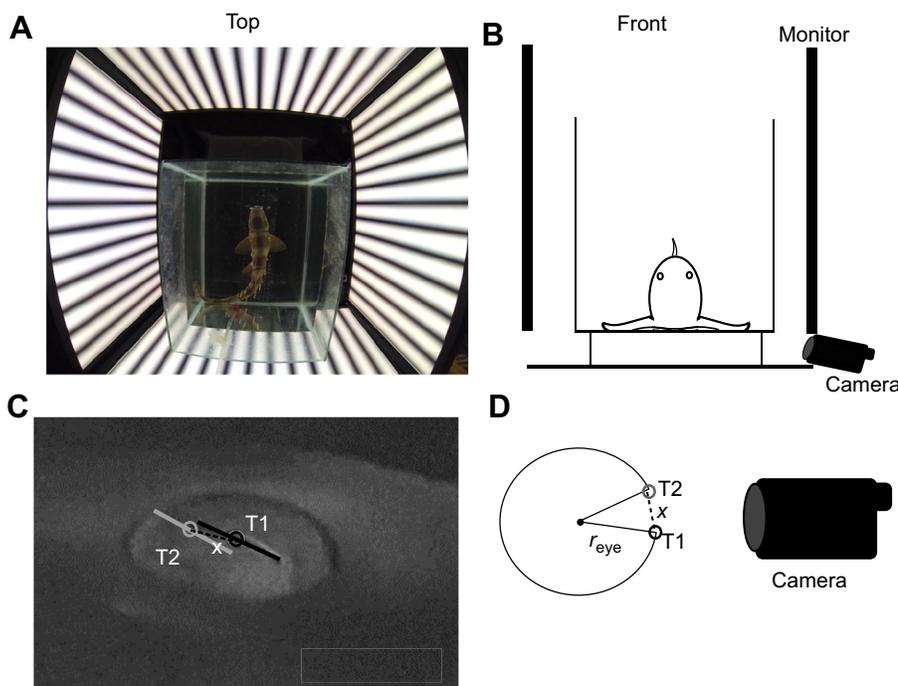


Fig. 1. Virtual optokinetic drum setup and calculation of eye movements. (A) Top view photograph of *Chiloscyllium punctatum* positioned at the centre of the virtual drum. The animal is surrounded by four computer monitors with vertical gratings, which move horizontally. (B) Position of the recording camera. The schematic shows a frontal view with the camera positioned underneath a side monitor and focused on the eye. (C) Eye movements were calculated in degrees by comparing the position of the pupil in one frame (T1) with the next frame (T2). (D) The inverse sine of the distance (x) the pupil moved and the radius of the eye (r_{eye}) were used to calculate eye movements per degree.

from How et al., 2007) to automatically track the position of the pupil. Spatial sampling resolution was half a pixel, equivalent to 0.05 deg in gaze rotation. Eye movements were calculated in degrees by comparing the relative position of the pupil between frames (Fig. 1C,D) and calibrating pixels for absolute size at the plane of the eye. Eye diameter was initially estimated as the maximum diameter of a circle fitted to the exposed eye. These estimates of eye diameter were later confirmed in euthanised individuals. The inverse sine of the distance (x) the pupil moved on screen and the radius of the eye (r_{eye}) was used to calculate eye movements in degrees (Fig. 1C,D). However, these calculations did not take into account the 3D path of the eye's rotation. However, given the small eye movements of the sharks, the error was estimated to be very small – approximately 0.2% for eye movement of 10 deg.

Experimental procedure

Sharks were acclimated to the experimental setup for 10 min. Each trial tested one particular spatial frequency and contrast combination and consisted of eight 10 s motion segments. Stimulus direction was reversed after each segment. The start direction for each trial (clockwise or anticlockwise) was chosen at random.

In a pilot study, we tested the ability of sharks to track gratings at different speeds. A vertical sine-wave grating with a spatial frequency of 0.14 cpd and speeds of 0.5, 1, 2, 5, 10, 20 deg s⁻¹ were used to estimate the tracking gain (i.e. the speed of the eye relative to the speed of the stimulus). Speeds were presented in a randomised order. The gain decreased with stimulus speeds above 5 deg s⁻¹; a speed of 2 deg s⁻¹ produced the most consistent eye movements with the highest and most reliable tracking gain (low s.e.m.) in both species and was used for all further experiments (Fig. 2).

Contrast sensitivity and spatial resolution

For each animal, a contrast threshold was determined for every spatial frequency. The contrast threshold was reached when the sharks no longer tracked the stimulus as judged by the fact that recorded eye movements were smaller than during control conditions, which were not expected to elicit stimulus-directed eye movements. For each individual, three different controls were used: (1) a high spatial frequency grating of 5 cpd, which is significantly greater than the anatomical estimates of spatial

resolving power for both species (Harahush et al., 2014; L. Peel, S.P.C. and N.S.H., unpublished data); (2) a stationary grating with a spatial frequency of 0.24 cpd (preliminary trials suggested that sharks were able to track a grating of this size); and (3) a moving zero contrast grating. At each spatial frequency, contrasts between 100% and 0.5% were tested in a randomised order. Spatial frequencies were tested in 0.1 log₁₀ unit steps between 0.017 and 0.640 cpd. The presentation order of spatial frequencies and contrasts within a spatial frequency was randomised.

To determine whether contrast sensitivity was affected by light intensity, the experiment was performed at two average light intensities – 3.2×10⁻⁵ W sr⁻¹ cm⁻² and 3.7×10⁻⁶ W sr⁻¹ cm⁻² (International Light Technologies, ILT1700) – adjusted by dimming the brightness of the monitors. At the dimmer light intensity, only two individuals of each species were tested and contrast sensitivity was estimated in 0.2 log₁₀ unit steps for spatial frequencies between 0.017 and 0.640 cpd. Pupil size (horizontal extent of the vertical slit pupils) was measured at both light intensities.

For all stimuli, the centre position of the pupil was tracked at 40 ms intervals over 80 s of stimulus movement (four 10 s segments for each direction). The horizontal component of the eye movement trace was smoothed with a Gaussian filter with a standard deviation of three frames. Large and fast eye movements, which generally represented saccades or other voluntary eye movements (defined as eye velocity that exceeded 2 deg s⁻¹), were removed to avoid contamination of slow phase eye movements, which represent the visual tracking phase. The remaining track was spliced back together and any offsets at the splice position were removed. If more than 4 s of tracking was removed from a single segment, it was excluded from further analysis. The remaining segments were then fitted by a straight line (Fig. 3A), which corresponds to the average eye velocity. The slopes of all segments that corresponded to the same stimulus direction were averaged to estimate average eye velocity for the clockwise and anticlockwise stimulus directions, respectively (Fig. 3B). Tracking gain was calculated by dividing the average of the absolute eye velocity by the stimulus velocity. The difference between the eye velocity for different stimulus directions was used to determine whether the animals tracked the stimulus. Calculating the difference in eye velocity between alternating stimulus directions made it easier to reject slow drifting eye movements at stimulus thresholds. For each individual, the maximum difference in relative eye velocity between stimulus directions during control conditions was used as the noise threshold to define the presence of tracking. Contrast thresholds were then calculated by interpolating the results to find the contrast at which the difference in eye velocity was equal to the noise threshold (Fig. 3C). Our experimental design of eight 10 s intervals with alternating movement directions helped optimise the sensitivity of our analysis, as it limited the number and impact of saccades on our estimates of optokinetic gain and helped separate random eye movements from stimulus-directed eye movements.

For each individual, a full contrast sensitivity function was calculated as the inverse of threshold contrast at each spatial frequency. The contrast sensitivity function was then averaged across animals. An ANOVA was performed in R (R Foundation for Statistical Computing, Vienna, Austria) to test for differences in peak contrast sensitivity between the two species and between light intensities. Spatial frequencies within 0.1 log₁₀ unit steps of the highest contrast sensitivity were used to compare peak contrast sensitivity between species and light intensities. Spatial resolution and contrast sensitivity were log₁₀ transformed for all analyses to fulfil the assumption of homogeneity of variance (Zar, 1999). The

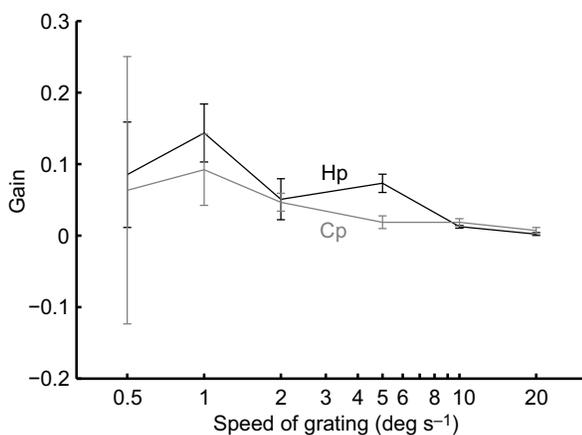


Fig. 2. Mean±s.e.m. gain of eye movements at different stimulus speeds. The effect of the speed of the horizontally moving 0.14 cpd vertical sine-wave grating on the gain in *Heterodontus portusjacksoni* (Hp) and *C. punctatum* (Cp) ($n=3$ for each species).

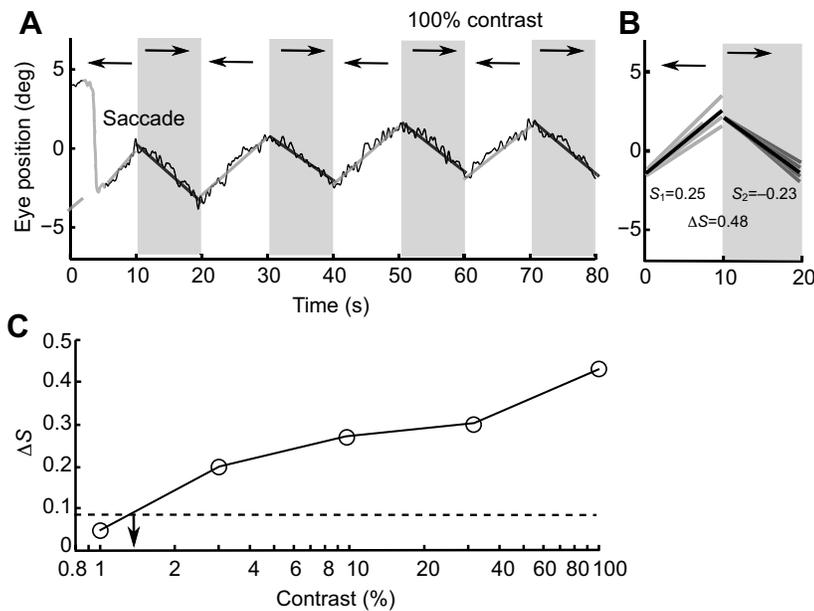


Fig. 3. Method for calculating average eye movements in order to calculate contrast sensitivity. (A) Eye movement trace from *H. portusjacksoni* in response to vertical sine-wave gratings at a spatial frequency of 0.18 cpd at 100% contrast, with a slope, corresponding the velocity of eye movements, fitted to each 10 s segment. The saccade is traced in grey as it was removed from the analysis. A decrease in the eye position represented tracking to the right and increases represent tracking to the left. (B) The eye velocity for each 10 s segment (grey) and average eye velocity (black) when the gratings moved to the left (S_1) or right (S_2) and the difference between the average relative eye velocity (ΔS). (C) The difference in relative eye velocity (ΔS) at 0.18 cpd at a range of contrast. The dashed line represents the noise threshold, which was estimated from the control stimuli. The arrow indicates the contrast threshold, calculated as the contrast at which the interpolated ΔS equaled the noise threshold.

highest spatial frequency at 100% contrast was used as an estimate of the spatial resolving power.

The effect of motion direction on eye movements

To understand the ability of sharks to use eye movements to compensate for motion in different directions, eye movements were recorded in response to three different types of large-field motion. (1) Horizontal motion of vertical sine-wave gratings rotating around the shark, simulating a rotation of the shark around the vertical axis. The horizontal motion stimulus was used to estimate contrast sensitivity. (2) Vertical motion, using a horizontal sine-wave grating that moved simultaneously on all monitors in a vertical direction and simulated visual motion consistent with a shark moving up and down in the water column. And (3) rotation around the longitudinal body axis of the shark (roll). During the presentation of the stimulus, which simulated a roll, horizontal sine-wave gratings were presented on the two monitors positioned along the side of the shark (monitors in front and behind the sharks were blacked out). The gratings moved in an upward direction on one monitor, whilst the gratings on the other monitor moved downwards. For all stimuli, gratings were presented at 100% contrast at two spatial frequencies (0.08 and 0.14 cpd) with a rotation speed of 2 deg s^{-1} .

As a comparison, four horizontally moving vertical black bars on a white background (one bar was presented on each monitor) were used to test the sharks' ability to track object motion. Movement speed was 2 deg s^{-1} and bar width was set at either 4 or 6 deg (approximately equivalent to the bar width of a 0.08 and 0.14 cpd grating, respectively). Tracking was assessed as described for the contrast sensitivity experiment.

Eye movements in free-swimming sharks

To determine whether eye movements were affected by restraining the animals, eye movements were also measured in three free-swimming *C. punctatum* housed in a $0.8 \times 1.5 \text{ m}$ clear, rectangular aquarium. Sharks exhibited a large degree of lateral head movement during swimming due to their sinusoidal swimming pattern. Eye movements were recorded on a Sony Handycam (HDR CX700), which was positioned perpendicular to

the swimming direction. Head movements were recorded simultaneously with a second Sony Handycam (HDR CX550), which was positioned directly above the tank. To measure the correlation between eye and body movements during swimming, the two cameras were synchronised to within one frame (error less than 20 ms). For each individual shark, three passes of the camera were analysed. Each pass encompassed approximately one swimming cycle. A swim cycle consisted of a head movement away from the midline to one side of the body. When the head reached the extremity, it then moved to the opposing side of the body before returning back to the midline.

Eye and head movements of free-swimming sharks were analysed as described above. To determine the relative movement of the eye within the head and remove translational motion, an additional marker point on the head next to the eye was tracked and pupil position calculated relative to the marker. Eye size was used to calculate eye movements in degrees (see above). Head rotations were measured with the camera above the tank by automatically tracking the position of the two eyes, which allowed head rotation to be calculated as an angle in the horizontal plane. Because the sharks were at different points in the swimming cycle with each pass of the camera, the correlation between head and eye movements was estimated using cross-correlations. The peak of the cross-correlation trace was normalised. A correlation value of one represented a perfect correlation between head and eye movements, while a value of zero meant no correlation. Cross-correlations from individual recordings were aligned along the time lag of the largest value and averaged.

RESULTS

Contrast sensitivity and spatial resolution

Both species of shark moved their eyes to follow the rotating grating; however, neither species performed a typical optokinetic response characterised by a rhythmic nystagmus (Fernald, 1985; Mandecki and Domenici, 2015). In contrast, saccades were sporadic, occurring at different points in the slow phase rotation, and were equally likely to move in the same direction as the slow phase eye movements as well as the opposite direction (Fig. 3A). Eye movements had a low gain, even during the

preliminary speed experiment. A gain of one, which would indicate tracking at the same angular speed as the stimulus, never occurred. Average gain was 0.21 and 0.06 for *H. portusjacksoni* and *C. punctatum*, respectively. For both species, tracking never completely stabilised gaze.

Despite the low gain, eye movements were reliable and increased consistently with grating contrast (Fig. 3C). Based on the threshold contrasts for all spatial frequencies, a contrast sensitivity function was calculated for each species (Fig. 4). Contrast sensitivity increased for both species with spatial frequency until approximately 0.14 cpd, before declining towards higher frequencies. In both species, the threshold for spatial resolving power was 0.38 cpd. No visual tracking occurred at higher spatial frequencies. The peak contrast sensitivity threshold was significantly higher for *H. portusjacksoni* than for *C. punctatum* (contrast sensitivity 75.4 versus 34.6, respectively; ANOVA, contrast sensitivity~species, $F_1=8.37$, $P=0.007$).

The approximately 10-fold difference in light intensity was enough to cause a significant increase in the size of the pupil for both species. The horizontal pupil diameter of *C. punctatum* increased from 3.7 ± 0.18 to 7.1 ± 0.92 mm (mean±s.e.m.; t -test, $t_3=-3.76$, $P=0.03$) and the horizontal pupil diameter of *H. portusjacksoni* increased from 9.7 ± 0.75 to 17.2 ± 0.81 mm (t -test, $t_3=-4.94$, $P=0.02$) when the light intensity was decreased. However, light intensity had no significant effect on contrast sensitivities (ANOVA, contrast sensitivity~species+light intensity, $F_1=2.71$, $P=0.11$).

Directional sensitivity of eye movements

We used a range of wide-field motion stimuli to determine whether sharks used eye movements to compensate for large-field image motion in different directions. Both *H. portusjacksoni* and *C. punctatum* produced slow but consistent and reliable eye movements in the direction of the moving gratings (Fig. 5). Both eyes were monitored for responses to the vertically moving stimuli. For both of the vertical motion stimuli, which simulated visual motion consistent with the rising or lowering of the shark in the water column and a rotation around the longitudinal axis of the shark, both eyes were able to follow the gratings, thereby moving in either the same or opposite directions, as required (Fig. 5). Eye movement gain did not vary between the wide-field stimulus conditions (ANOVA, gain~species+grating, $F_2=3.01$, $P=0.07$), but *H. portusjacksoni*

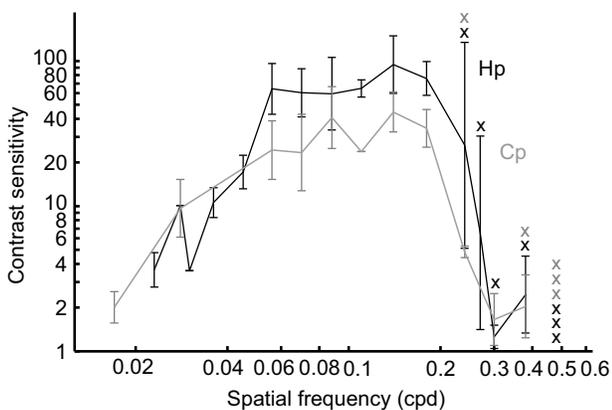


Fig. 4. Comparison of the contrast sensitivity function between *H. portusjacksoni* (Hp) and *C. punctatum* (Cp) at a light intensity of $3.2 \times 10^{-5} \text{ W sr}^{-1} \text{ cm}^{-2}$, showing the contrast sensitivity (mean±s.e.m.) at each spatial frequency. The 'X' markers represent an individual that did not exhibit tracking at a specific spatial frequency.

produced eye movements with significantly greater gain ($0.21 \pm 0.03 \text{ deg s}^{-1}$, mean±s.e.m.) than *C. punctatum* ($0.06 \pm 0.01 \text{ deg s}^{-1}$) (ANOVA, gain~species, $F_1=29.01$, $P<0.0001$). During the object motion stimulus, only one individual of *H. portusjacksoni* and one individual of *C. punctatum* tracked the object with their gaze.

Eye movements during free-swimming

Chiloscyllium punctatum did not display any compensatory eye movements to correct for the lateral displacement of the head during sinusoidal swimming (Fig. 6A). A cross-correlation analysis was performed, but showed no evidence of a peak that would indicate a correlation between head and eye movements (Fig. 6B, solid line). Thus, during swimming, sharks would experience retinal slip owing to head movements.

DISCUSSION

Contrast sensitivity and spatial resolution

The benthic sharks *H. portusjacksoni* and *C. punctatum* both responded to moving gratings with small but reliable eye movements, which allowed us to accurately estimate their contrast sensitivity function (Fig. 4). Both species had poor spatial resolution (0.38 cpd), but high sensitivity to contrast. Contrast sensitivity in both *H. portusjacksoni* and *C. punctatum* peaked at a spatial frequency of 0.14 cpd. *Heterodontus portusjacksoni* was capable of detecting contrast as low as 1.3%, compared with 2.9% in *C. punctatum* (Fig. 4). The difference in contrast sensitivity may be attributed to *H. portusjacksoni* having a pure rod retina (Hart et al., 2011; Schieber et al., 2012) and wider rods than *C. punctatum* (Schieber et al., 2012), increasing light sensitivity, which should be beneficial for detecting contrast (Land and Nilsson, 2012). The higher contrast sensitivity in *H. portusjacksoni* is thus likely an adaptation to the lower light levels this species experiences in its temperate environments (McFarland, 1990) compared with *C. punctatum*, which occupies tropical environments (Last and Stevens, 2009; Froese and Pauly, 2013). However, the sensitivity of *H. portusjacksoni* to light may come at a cost to temporal resolution (Ryan et al., 2016), rather than acuity, as spatial resolving power is similar in both species.

An almost 10-fold drop in stimulus brightness did not influence contrast sensitivity. The similarity between the contrast sensitivity functions at the two intensities was not unexpected, as in humans, contrast sensitivity has been found to be unaffected by luminance except at the threshold of light sensitivity, when photoreceptor function is sub-optimal (Paulsson and Sjostrand, 1980; Mustonen et al., 1993). The light intensities tested are likely to be within the normal range of intensities experienced by both shark species and reflect light experienced in approximately the first 10–20 m of the water column during the middle of the day (Lythgoe, 1988; Cronin et al., 2014). However, similarity in the contrast sensitivity curves provides confidence about the shape and peak of the contrast sensitivity for the two shark species investigated and suggests the low spatial resolution and low eye movement gain are not due to light sensitivity or photobleaching.

Our estimates of spatial resolving power (0.38 cpd; Fig. 4) were much lower than existing anatomical estimates, i.e. 2.9 cpd in *C. punctatum* (Harahush et al., 2014) and 3.1 cpd in *H. portusjacksoni* (L. Peel, S.P.C. and N.S.H., unpublished data). Estimates based on retinal ganglion cells tend to overestimate spatial resolving power, as ganglion cell counts often include amacrine cells displaced to the ganglion cell layer and specialised ganglion cells that do not contribute to visual acuity, such as giant ganglion cells (Stell and Witkovsky, 1973; Anctil and Ali, 1974; Stell et al., 1975; Bozzano and Collin, 2000). However, our optokinetic estimates were eight to

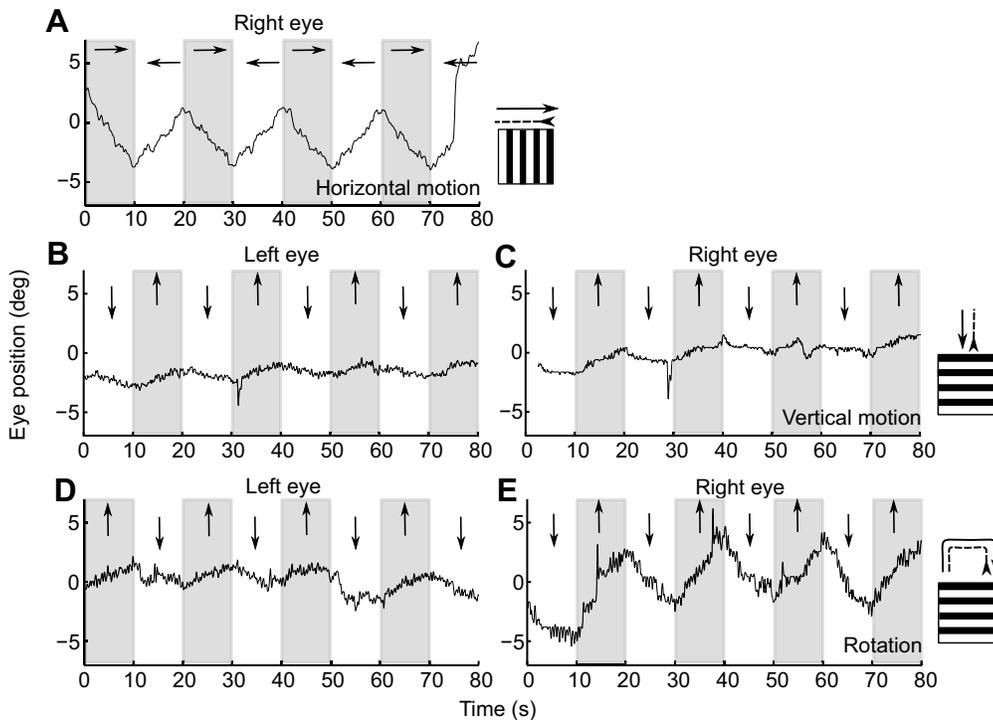


Fig. 5. Eye movements as a function of stimulus direction. (A) Eye movements of a *H. portusjacksoni* in response to horizontally moving vertical sine-wave gratings. Arrows demonstrate the horizontal direction (left or right) of the moving grating. For vertical gratings, a decrease in eye position represents movement to the right and an increase in eye position represents movement to the left. (B) Left and (C) right eye movements from *H. portusjacksoni* in response to a vertical motion stimulus (horizontal sine-wave grating moving up or down on all monitors simultaneously). For horizontal gratings, a decrease in eye position represents a downward eye movement and an increase represents an upward movement. (D) Left and (E) right eye position from *H. portusjacksoni* in response to rotation around the longitudinal body axis of the shark (the horizontal gratings on the two lateral monitors were moved in opposite directions).

10 times lower than anatomical estimates, a much larger than expected difference (Stell et al., 1975). There are a number of experimental factors that may have led to an underestimation of the optokinetic responses (both gain and resulting estimates of spatial resolution), such as the amount of the visual field the stimulus covered (Wyatt and Pola, 1987), the presence of non-rotating monitor edges (Wyatt and Pola, 1987), the restraint of the animals during the experiment (Dieringer et al., 1983; Gioanni, 1988), as well as a lack of attention towards the stimulus by the animals (Wyatt and Pola, 1987). However, a more likely explanation of the low threshold estimates is that the optomotor system in these species is not sensitive to high spatial frequencies. The optomotor system is designed to counteract image rotations. Estimating image rotations is easiest when viewing distant objects that are less affected by translational self motion and less affected by object motion (distant objects produce, on average, slower retinal speeds). In the underwater environment, distant objects do not contain high spatial frequencies because of the fast degradation of image contrast and blurring with viewing distance (Lythgoe, 1980, 1988; McFarland, 1990; Land and Nilsson, 2012). Low spatial frequency tuning of the optomotor system would therefore allow the system to preferentially ignore close objects (Land, 1999; Eckert and Zeil, 2001). This argument would explain why our results show such a sharp decline in the contrast sensitivity function at spatial frequencies above 0.18 cpd (Fig. 5).

An alternative method to calculate spatial resolving power, which is less affected by the low sensitivity of the optomotor system to high spatial frequencies, has been provided by da Silva Souza et al. (2011). da Silva Souza et al. (2011) have shown that in other vertebrates, the peak of the contrast sensitivity curve (CS_{peak}) correlates with the threshold of spatial resolution (SRP):

$$\text{SRP} = 11.47 \times e^{2.18 \times \log_{10}(CS_{\text{peak}})}. \quad (1)$$

Using Eqn 1, we can estimate the spatial resolving power of both shark species studied to be approximately 1.8 cpd (based on the

peak of the contrast sensitivity curves at 0.14 cpd), which is a much better fit of the anatomical estimates. Further behavioural experiments are clearly needed to resolve this issue.

Both *H. portusjacksoni* and *C. punctatum* have relatively low spatial resolving power in comparison to teleosts, such as the goldfish, *Carassius auratus* (Northmore and Dvorak, 1979), and the bluegill, *Lepomis macrochirus* (Northmore et al., 2007) (Fig. 7A), and most other vertebrates (Prusky et al., 2004; Rinner et al., 2005; Tappeiner et al., 2012) (Fig. 7B), but are more sensitive to contrast. Only primates have greater contrast sensitivity (Miller et al., 1980; Schor and Levi, 1980). The rod-dominated retina of sharks (Harahush et al., 2009; Hart et al., 2011; Schieber et al., 2012) may play an important role in increasing contrast sensitivity, but may come at the cost of low spatial resolution. Harbour seals, *Phoca vitulina* (Hanke et al., 2011), and goldfish, *C. auratus* (Northmore and Dvorak, 1979), both of which are aquatic animals with rod-dominated retinas (Jamieson and Fisher, 1971; Stell and Hárosi, 1976), have contrast sensitivity functions most similar to the sharks studied here, suggesting contrast is of particular importance in aquatic animals.

Eye movements in sharks

Owing to the structure of the marine environment, important visual motion occurs in a number of orientations. Therefore, it is not surprising that the sharks in this study tracked sine-wave gratings simulating different forms of self motion. Our results were equivalent to eye movements recorded from dogfish, *Mustelus californicus*, when the sharks were physically moved (Maxwell, 1920). However, when the semicircular canals and otoliths were removed from *M. californicus*, no compensatory eye movements occurred, suggesting optokinetic responses are exclusively driven by vestibular responses (Maxwell, 1920). Our results on stationary benthic sharks suggest eye movements are not entirely dependent on whole-body movement, but can be elicited purely by visual information.

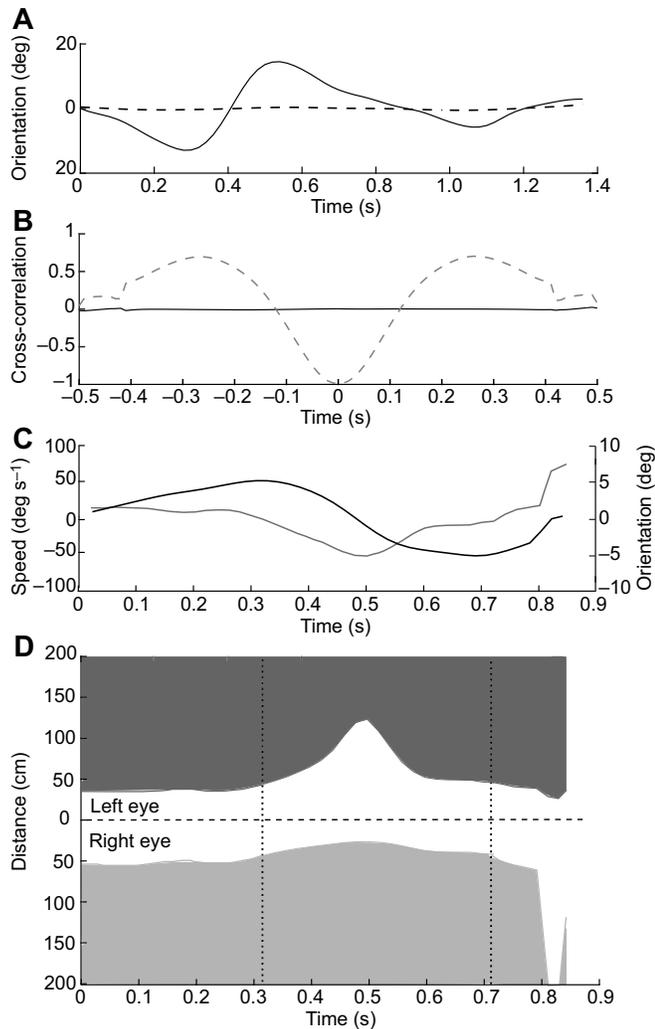


Fig. 6. Analysis of head and eye movements of *C. punctatum* during free-swimming. (A) An example of the head (solid line) and eye (dashed line) movements during a swim cycle. (B) Average cross-correlation for head movements against eye movements. The solid line represents the results of the cross-correlation performed on head movement against the eye movements. To give a sense of scale, the dashed line represents a theoretical example of a shark that fully compensates head rotation with corresponding eye movements. (C) The average head movement during the sinusoidal swimming (black line) and the average corresponding rotational speed of head movements (grey line). (D) The distance at which an object would not appear blurred for *C. punctatum* during free-swimming, based on average head movements. The shaded areas of the left eye (light) and right eye (dark) express the distance that would not be blurred based on a swimming speed of 0.32 m s⁻¹. Objects falling within the clear area close to the shark would be blurred on the retina. The dashed line represents the midline and dotted lines represent when the midline was crossed.

The eye movements in response to vertical motion stimuli demonstrated that the sharks were capable of rotating their eyes in opposite directions. Our findings support the existence of a monocularly organised oculomotor system in sharks (Maxwell, 1920; Masseck and Hoffmann, 2008). Monocular organisation is more common in animals with laterally positioned eyes as described for some teleost fishes [sandlance, *Lymnichthyes fasciatus*, and pipefish, *Corythoichthyes intestinalis* (Fritsches and Marshall, 2002; Pettigrew et al., 1999)] and the chameleon, *Chamaleo chamaleo* (Gioanni et al., 1993; Pettigrew et al., 1999). The contralateral placement of the medial rectus motor neurons in the

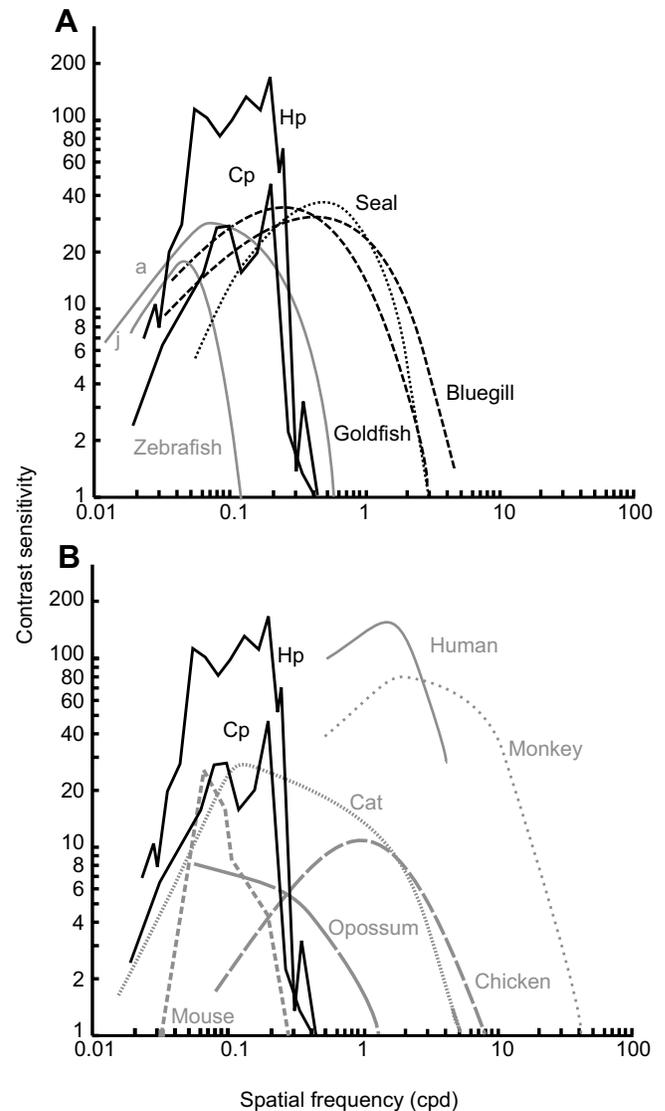


Fig. 7. Contrast sensitivity functions of *H. portusjacksoni* (Hp) and *C. punctatum* (Cp) compared with a range of vertebrates. (A) Comparison of sharks at a light intensity of $3.2 \times 10^{-5} \text{ W sr}^{-1} \text{ cm}^{-2}$ with marine vertebrates (Northmore and Dvorak, 1979; Rinner et al., 2005; Northmore et al., 2007; Hanke et al., 2011; Tappeiner et al., 2012). Zebrafish measurements were made from optokinetic drum experiments in both adults (a) and juveniles (j). Harbour seal, goldfish and bluegill contrast sensitivity functions are estimated using other methodologies. (B) Comparison of sharks with other vertebrates (Donaghy, 1980; Miller et al., 1980; Schor and Levi, 1980; Silveira et al., 1982; Prusky et al., 2004; Jarvis et al., 2009). Contrast sensitivity function measurements for these vertebrates were made in optokinetic drum experiments.

midbrain of sharks differs from most vertebrates, which may allow eye movements to be controlled independently (Graf and Brunken, 1984).

One surprising result of our study was the extremely low gain of the optokinetic system. Even the fastest eye movements were much slower than the speed in which the stimuli moved (gain of 0.21 and 0.06 in *H. portusjacksoni* and *C. punctatum*, respectively). In contrast, juvenile zebrafish, *Danio rerio*, are capable of tracking a grating of 2.4 deg s⁻¹ with a gain of 0.9 (Easter and Nicola, 1997). The gain of the sharks was more similar to that of other vertebrates that produce independent eye movements (*L. fasciatus*, gain=0.52,

Fritsches and Marshall, 2002; *C. chameleon*, gain=0.35, Gioanni et al., 1993).

The low gain may reflect the retinal topography of ganglion cells. Both species of sharks examined in this study have horizontal visual streaks (Harahush et al., 2009; Schieber et al., 2012), which reduces the need to perform large and fast eye movements in order to stabilise objects on the area of the retina with the greatest resolution (Hughes, 1977). However, many species with visual streaks still perform significant eye movements (Hughes, 1971; Harris, 1965). Thus, the low gain of the two shark species may instead relate to their more primitive visual structure (Shirai, 1992, 1996; Winchell et al., 2004) and more modern vertebrates may have developed more specialised optokinetic responses.

Optic blur

In contrast to previous research (Smith, 2006; Osmon, 2008; McComb et al., 2009), free-swimming *C. punctatum* showed no evidence of compensatory eye movements, despite strong lateral head rotations. This result is consistent with the low gain found in the drum experiment and means that *C. punctatum* will experience regular periods of optic blur during swimming. The angular velocity (S) of an image that would incur significant blur in the shark's eye can be calculated based on the receptor acceptance angle ($\delta\rho$) and the response time of the retina ($\delta\tau$) (Land, 1999):

$$S = (\delta\rho/\delta\tau). \quad (2)$$

Dividing the acceptance angle ($\delta\rho$) by the difference in stimulus speed and the speed of the eye movements (S), we can determine the response time necessary to avoid image blur:

$$\delta\tau = (\delta\rho/S). \quad (3)$$

We used Eqn 3 to determine the photoreceptor response time required to avoid image blur in *C. punctatum*. During the optokinetic experiment, the average angular speed difference between the stimulus and the eye was 1.88 deg s⁻¹. With an acceptance angle of 2.6 deg and a spatial resolving power of 0.38 cpd, *C. punctatum* would need to have very slow photoreceptors with a response time of >1000 ms to experience significant motion blur. This response time is much slower than response times measured in other species of sharks (23–35 ms) (McComb et al., 2010). Therefore, it is unlikely *C. punctatum* experienced significant image blur during the optokinetic drum experiments.

During free-swimming, the maximum rotational speed at which *C. punctatum* moved their heads was 256 deg s⁻¹. To avoid image blur, during the maximum speed of head rotation, *C. punctatum* would need a response time of approximately 10 ms, suggesting that *C. punctatum* experienced motion blur during swimming. Insufficient time to process images causes a loss of valuable spatial and contrast information, thus impeding object detection and recognition. However, motion blur during swimming may be periodic. The forward movement during swimming means that head movements away from the midline will reduce image motion across the retina of the eye leading the rotation by counteracting forward motion. However, as the shark moves the head back towards the midline, the translational and rotational components of image motion across the same retina will combine and increase blur (Harris, 1965; Land, 1999, 2015). Based on a photoreceptor response time of 32 ms (McComb et al., 2010), a swimming speed of 0.32 m s⁻¹ (Ryan et al., 2015), a spatial resolving power of 0.38 cpd and average head rotations (Fig. 6C), objects farther away

than 35 cm would only blur for approximately 10% of the swim cycle (Fig. 6D). However, if spatial resolution was greater than 0.38 cpd, *C. punctatum* would experience more blur. Using the spatial resolving power estimate of 1.8 cpd, objects farther away than 35 cm would be blurred during 43.9% of the swim cycle. This may be acceptable for a relatively sedentary species such as *C. punctatum*, but more active and faster sharks may require greater compensatory eye movements. One advantage of head movements without compensatory eye movements is in extending the area of the visual field and reducing the blind spot behind the shark (McComb et al., 2009). However, this may be at the expense of periodic blurring. The interactions between swimming, head movements and eye movements are essential in understanding how sharks perceive their visual world, and an assessment of eye movements in a range of free-swimming species of sharks is required, both in the natural environment and with artificial visual stimuli.

In summary, optokinetic drums are a useful method for assessing eye movements and estimating contrast sensitivity and spatial resolving power in benthic sharks. Both species of benthic shark, *H. portusjacksoni* and *C. punctatum*, assessed in this study were very sensitive to contrast, suggesting that sharks do not have 'poor' vision as once thought, but are optimised to the low-contrast aquatic environment. In addition, the results suggest that some sharks may not completely stabilise gaze, and, when swimming, may go through periods of stabilised and blurred vision, but increase their visual field.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

L.A.R. carried out the experiments, participated in data analysis, conception and design of the study, and drafted the manuscript. N.S.H. and S.P.C. participated in the conception and design of the study, interpretation of the data, and helped draft the manuscript. J.M.H. designed the software used for tracking eye movements, participated in data analysis, conception and design of the study, and interpretation of the data, and helped draft the manuscript.

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